

Effects of patch type and food specializations on fine spatial scale community patterns of nocturnal forest associated Lepidoptera

Jürgen Kusch

University of Kaiserslautern, Department of Ecology, Kaiserslautern, Germany

E-mail: kusch@rhrk.uni-kl.de

Christine Goedert, Marc Meyer

Musée national d'histoire naturelle, 25 rue Münster, Luxembourg

Abstract. Species groups at different sites may build a meta-community that owns characteristic patterns of species distribution. Local differences, species interactions, random effects and dispersal characteristics can influence the diversity of local insect communities. We measured the diversity of nocturnal Lepidoptera at 12 sites of a temperate mixed forest that represented different patch types. To analyze causes of community structures, we tested for nestedness, checkerboards, clementsian, gleasonian, or evenly spaced gradients, and for random distribution as hypothetical patterns of a meta-community. The most diverse sites were patches at outer and inner edges of the forest. Lowest diversity was observed at a clearance inside the forest, and at three of four grove patches outside the forest. A cluster analysis of the similarity of Lepidoptera communities at different sites showed that the patch type and location, inside the forest (clearings, inner edge) or outside the forest (groves, outer edge), influenced the community structure. With increasing similarity of plant species growing at two sites, the faunal similarity of those two sites increased not significantly, indicating that differences of local plant communities caused a minor part of the faunal variation. The Lepidoptera communities were clearly nested, and different forms of gradients were detected in various subgroups of the Lepidoptera communities. Whereas nestedness indicated that patches were statistically depauperate subsets of the regional fauna, gradients showed that environmental changes between patches were responsible for different communities at that patches. Checkerboards and random distribution were not observed at all. This showed that interspecific competitions, as well as purely stochastic factors were not the driving forces in community regulation.

Key words: Communities, community patterns, food specialization, forest, gradient, nestedness, patch type, spatial distribution.

INTRODUCTION

The recognition of patterns in communities and of the causes of distribution and abundance of species as the most important determinant of natural community structure and composition is a central goal in community ecology. Ecological communities at different sites may build a meta-community that owns characteristic patterns of species distribution. Local and regional differences may transfer into the diversity of local communities, and the determinants of species richness of local communities are of large interest in research of the recent years (Zobel 1997; Hillebrand & Blenckner 2002).

Patterns that were observed in communities are at

least six that describe in an idealized way the distribution of species among sites, when species are ordered into a site by species matrix (Leibold & Mikkelsen 2002). Nested distributions occur, when species compositions on less rich sites are proper subsets of those on richer sites. Patterson & Atmar (1986) proposed to count the number of naturally occurring gaps, defined as species absences where species should have occurred in larger subsets, and used the number of gaps as a test statistics. So, a nested pattern occurs whenever the species observed in depauperate habitat patches are a subset of those found in more species-rich patches. A checkerboard distribution arises when certain species always competitively exclude each other. Species pairs then

have mutually exclusive distributions, but such pairs occur independently of other pairs (Diamond 1975). Clementsian gradients result in discrete communities that replace each other as a group (Clements 1916). Gleasonian gradients result in species turnover, but the arrangement of species ranges along the gradient is random (Gleason 1926). No discrete communities result in evenly spaced gradients but species ranges are arranged more evenly than expected by random chance (Tilman 1982). At random distributions there are no gradients or other patterns in species distributions among sites (Simberloff 1983). Each species may then be distributed independently of other species, causing a continuum, and all species have identical extinction probabilities at a site.

Community patterns represent idealized characteristics and result from diverse biogeographical and ecological processes. The diversity in local assemblages can be regulated by regional factors such as history of climate, evolution and migration and by local factors such as competition, predation, disturbance, or abiotic conditions (reviewed by, e. g., Hillebrand & Blenckner 2002). Differences in ecological specializations may influence the relative abundance of closely related butterfly species (Thomas 1995; Pullin 1995; Hughes 2000). Yet, for communities of Lepidoptera and Tenthredinoidea, Futuyma & Gould (1979) observed that few plant species in a deciduous forest had a highly distinct, specialized fauna. Various additional factors like patch isolation, temporal environmental stochasticity and dispersal limitations due to spatial constraints influence the colonization and abundance of Lepidoptera (e. g., Cappuccino & Martin 1997; Sutcliffe *et al.* 1997; Gutiérrez *et al.* 1999; Kitahara *et al.* 2000; Steffan-Dewenter & Tschamntke 2000; Petit *et al.* 2001; Nekola & Kraft 2002; Wahlberg *et al.* 2002).

Nestedness as a result from a wide array of such factors was observed in several butterfly communities (Fleishman & Murphy 1999; Summerville *et al.* 2002) and occurs also at fine spatial scales (Summerville *et al.* 2002). Other community patterns may occur as a result from species interactions as well as from spatial habitat changes. Furthermore, most investigations so far focused on species of grassland habitats. We therefore measured the patterns that occurred in Lepidoptera communities of different patches inside and nearby a forest in Luxembourg, Western Europe. We used different statistical tests developed by Leibold & Mikkelsen (2002) as well as by Atmar &

Patterson (1993, 1995) to detect nestedness, random and clumped distributions, or gradients. Effects of the degree and kind of host specializations of caterpillars of the observed Lepidoptera, as well as of taxonomical relations of species, on the type of community patterns were analyzed. To evaluate the importance of host specializations of caterpillars in determining the observed community patterns we also measured correlations of faunal and floral community similarities. We analyzed species occurrences at different patch types (clearances, inner and outer edge of forest, and groves nearby the forest) to determine effects of habitat changes on community patterns. Existing theory and our empirical data are discussed concerning which mechanisms are influential for the regulation of Lepidoptera communities in general and for the study system in particular.

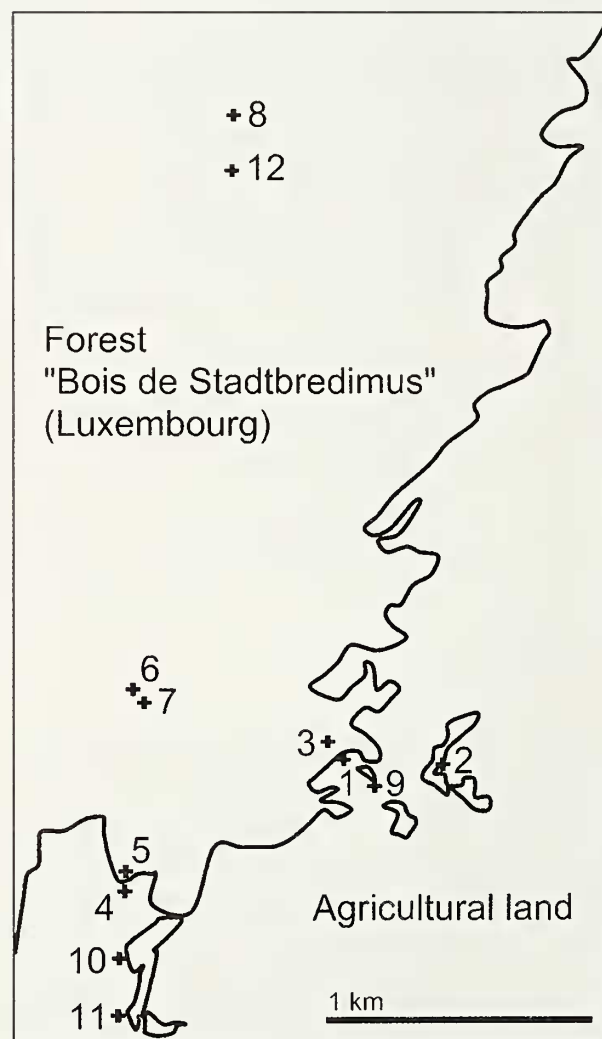


Fig. 1. Positions of sites at the forest "Bois de Stadtbredimus" (Luxembourg), where Lepidoptera species and the vegetation were investigated.

METHODS

Study area

Lepidoptera species and the vegetation were studied at 12 sites (Fig. 1) at the forest „Bois de Stadtbredimus“ in the south east of Luxembourg, Western Europe. Six of the 12 sites in each case represented one transect, reaching from clearances inside the forest (sites 6, 7, 8, 12) to the inner (3, 5) and outer edge of the forest (1, 4) and to groves lying outside the forest nearby (9, 10), or in larger distance (2, 11).

At sites 1 and 3 the forest is dominated by *Fagus sylvatica*, with *Hedera helix* covering large areas of the understory. At the forest edges *Prunus spinosa*, *Cornus sanguinea*, *Crataegus monogyna* grew outside, with *Quercus robur* and *Acer campestre* inside the edges. Outside the forest grassland covered most of the area, with *Arrhenatherum elatius*, *Anthoxanthum odoratum*, *Avenella flexuosa*, *Avenula pubescens*, *Lolium perenne* and *Poa trivialis* as the dominating grass species, and *Achillea millefolium*, *Lotus corniculatus*, *Medicago lupulina*, *Myosotis ramosissima*, *Veronica arvensis* as common herbs. At site 9 the edge of the grove was build by apple trees (*Malus sylvestris*), riddled with *Rosa* species, *Prunus spinosa* and *Sambucus ebulus*.

Fagus sylvatica and *Quercus robur* grew at sites 4 and 5 of the forest, with low numbers of flowering plants. The outer edge of the forest was build here by *Prunus spinosa* and *Carpinus betulus*. A pasture was located outside this site of the forest, with *Arrhenatherum elatior*, *Holcus lanatus*, *Lolium perenne*, *Poa trivialis* as grasses, and herb species like at sites 1 and 3. *Robinia pseudo-acacia* with *Rosa* sp. and *Prunus spinosa* grew at the groves of sites 10 and 11.

At sites 6 and 7 the tree species *Carpinus betulus* and *Quercus petraea* dominated the forest. Besides several grass species, *Sarothamnus scoparius*, *Populus tremula*, *Salix caprea*, *Rubus idaeus* and many *Rubus fruticosus* grew on the clearance area, where the two sampling sites were located.

Carpinus betulus, *Quercus petraea*, *Q. robur*, *Alnus glutinosa* and *Picea abies* were present at sites 8 and 12, as well as the bushes *Rubus fruticosus* and *Corylus avellana*. Among many grass species, herbs like *Leucanthemum vulgare*, *Galium mollugo*, *Rumex sanguineus*, *Anemone nemorosa* and *Geranium robertianum* grew on this clearance.

Sampling

Lepidoptera species were sampled seven times in the year 2001, simultaneously at all 12 sites once per month from April to October. The insects were captured during the nights by light trapping. These light traps with a fluorescent tube of 15 W power and a light emission spectrum of 320-480 nm wave length (super-actinic lights) were fixed in 1 m height above ground. Attracted insects fell into funnel pitfalls where they were killed by chloroform. To get early as well as late flying species the traps sampled from sundown to dawn. Macrolepidoptera were determined to species, using genital preparations where necessary (e. g., in the genera *Mesopamea* and *Oligia*). The Lepidoptera species list was deposited by Goedert et al. (2003). Species were ordered in caterpillar host plant guilds and in groups of different degrees of food specializations (monophag, one host plant species; oligophag, 2 to 5 host species; polyphag, >5 host species) according to Ebert (1994-2001), Koch (1991) and Fajcik & Slamka (1996).

Plants were determined two times at each sampling site, in May and July. Vegetation cover was determined according to Braun-Blanquet (1964).

Diversity measures

The relative abundance of species was calculated as the abundance of one species in relation to the total individual number of all species of the investigated community. The “frequency of species” is given as the relative number of sites, where a species was present. Similarity of communities was calculated by the Sorensen-index S , with

$$S = \frac{2C}{A+B}$$

where C is the number of species present in both of two compared communities, and A , B are the number of species present in community A , or B .

The α -diversity was determined by the Shannon-Index H_s , with

$$H_s = -\sum \left(\frac{n_i}{N} \right) \ln \left(\frac{n_i}{N} \right)$$

where n_i is the abundance of species i , and N is the total number of individuals in the community.

The Evenness-index, or Shannon's equitability, is given by

$$E_s = \frac{H_s}{H_{\max}}$$

where S is the total number of species of a community; $H_{\max} = \ln S$.

A cluster analysis of similarity of Lepidoptera communities was done for presence absence data and the Euclidean distances on the basis of the list of species that occurred at the different patches. Ward's method was used for group linkage.

Testing for community patterns

We first tested for a nested distribution of all species by the nestedness temperature calculator (Atmar & Patterson 1995). We then tested for nestedness as well as for five further hypothetical patterns of species' distribution among sites (checkerboards, clementsian, gleasonian, evenly spaced gradients and random distribution) according to Leibold & Mikkelsen (2002). Coherence, turnover and boundaries refer to three aspects of an incidence matrix that characterize each pattern. Coherence was calculated by the occurrence of embedded absences in ordinated matrices. Species turnover was indicated by the number of times one species replaces another between two sites ("Replacements"). Boundary clumping was indicated by Morisita's Index. The statistical tests of coherence, species turnover and boundary clumping are explained in detail by Leibold & Mikkelsen (2002). Occurrence of patterns was tested for all Lepidoptera species, for different taxonomical groups, for groups of differential degrees of food specializations of caterpillars (polyphagous, oligophagous, monophagous), and for different types of host plant specializations. A software program based in Excel to conduct these tests was kindly supplied by M.A. Leibold, Dept. of Ecology and Evolution, University of Chicago. Mantel tests were done with the help of the software PopTools (version 2.5.9; Hood, G. M. 2003; <http://www.cse.csiro.au/poptools>).

RESULTS

Diversity at different patches

We observed 325 Lepidoptera species, with a total of 5893 individuals, as well as 247 plant species at the

12 sites of the investigated forest region. Calculation of nestedness temperature showed that the distribution of Lepidoptera species among the 12 sites was clearly nested ($p [T < 41.36^\circ] = 1.24^{30}$, run count=100, average temperature=65.78°, std. dev.=2.08°). Island reorganization vectors gave a row position of study sites as it is given in Table 1, where site 1 is the most species rich. Most diverse sites were patches at outer and inner edges of the forest, as well as patch 2 at a grove's edge. Diversity was lowest at a clearance inside the forest, and at three of the four grove patches outside the forest. The Lepidoptera species number at individual patches varied from 176 to 73, with total abundances being 804 respectively 166. Plant species number varied from 71 at patch 1 and 74 at patch 12, to 37 at patch 3. Obviously a correlation of Lepidoptera species number and plant species number or vegetation cover did not occur (Table 1; pearson correlation: $p=0.7420$).

Patch location and caterpillar host plants

A cluster analysis of the similarity of Lepidoptera communities at the different patches showed that communities at similar patches were grouped together (Fig. 2). All four patches at clearances as well as two patches at inner edges of the forest built one of two main groups; outer edges and grove patches built the second group. This indicated that the general patch type or location, inside or outside the forest, determined the communities. Whether the plant species growing at the different sites influenced the presence of Lepidoptera species, was analyzed by a comparison of floral and faunal similarities of communities (Fig. 3). With increasing similarity of plant species growing at two sites, the faunal similarity of those two sites increased slowly, explaining at best a minor part of the faunal variation only. A Mantel test revealed, that the dissimilarities of fauna and flora at two sites were not significantly correlated ($p=0.08$ for a positive correlation of faunal and floral dissimilarities). The extent of floral differences as well as of faunal differences of two sites also did not significantly depend on the geographical distance of that sites (Mantel test: $p=0.0775$ for a positive correlation of floral dissimilarity and geographical distance; $p=0.115$ for a positive correlation of faunal and geographical distance).

The relative number of Lepidoptera species that are specialized to different caterpillar host plants, did

Table 1. Patch types and characteristics of vegetation and Lepidoptera communities. Patches are arranged according to the island reorganization vectors of a nestedness calculation of all determined 327 Lepidoptera species. No. 1 is the most species rich patch, whereas least species inhabit patch no 12. Abundance values are numbers of individuals at a patch registered during seven catches between end of April and October of 2001. (ld, large distance to forest = 0.8-1.0 km; sd, short distance to forest = 0.2-0.3 km; H_s , Shannon-Index; E_s , Evenness-index; RA, Relative abundance of species; F, frequency of species at patches; $H_{max} = \ln S$)

Patch		Vegetation cover					Lepidoptera species						
No	Type	Plant sp. number	Tress %	Bushes %	Herbs %	Number	Abundance	Diversity H_s	Evenness E_s	H_{max}	Most abundant species	RA %	F %
1	Outer edge of forest	71	40	16	44	176	804	4.46	0.86	5.17	<i>Noctua pronuba</i>	8	100
											<i>Cyclophora linearia</i>	6	100
											<i>Campaea margaritata</i>	6	100
2	Edge of grove, ld	52	10	15	75	156	687	4.28	0.85	5.05	<i>Xestia c-nigrum</i>	7	100
											<i>Ochropleura plecta</i>	5	100
											<i>Epirrhoe alternata</i>	4	100
3	Inner edge of forest	37	50	20	30	147	847	4.23	0.85	5.00	<i>Cyclophora linearia</i>	8	100
											<i>Noctua pronuba</i>	6	100
											<i>Cyclophora annularia</i>	5	67
4	Outer edge of forest	87	44	15	41	138	484	4.28	0.87	4.93	<i>Xestia c-nigrum</i>	7	100
											<i>Cyclophora linearia</i>	7	100
											<i>Noctua pronuba</i>	5	100
5	Inner edge of forest	44	42	22	36	135	599	4.17	0.85	4.91	<i>Cyclophora linearia</i>	14	100
											<i>Cyclophora annularia</i>	5	67
											<i>Noctua pronuba</i>	5	100
6	Edge of clearing	65	42	20	38	129	381	4.36	0.90	4.86	<i>Noctua pronuba</i>	6	100
											<i>Calliteara pudibunda</i>	6	92
											<i>Mythimna impura</i>	6	83
7	Clearing, mean part	51	0	40	60	125	421	4.05	0.84	4.83	<i>Mythimna impure</i>	17	83
											<i>Noctua pronuba</i>	6	100
											<i>Deltote deceptor</i>	5	42
8	Edge of clearing	74	46	15	39	101	454	3.96	0.86	4.62	<i>Hypomecis roboraria</i>	6	75
											<i>Asteroscopus sphinx</i>	6	83
											<i>Campaea margaritata</i>	6	100
9	Edge of grove, sd	51	21	15	64	112	404	4.09	0.87	4.72	<i>Xestia c-nigrum</i>	10	100
											<i>Agrotis exclamationis</i>	6	92
											<i>Ochropleura plecta</i>	5	100
10	Edge of grove, sd	55	11	16	73	98	351	3.80	0.83	4.58	<i>Xestia c-nigrum</i>	16	100
											<i>Ochropleura plecta</i>	8	100
											<i>Mythimna impura</i>	6	83
11	Edge of grove, ld	53	19	10	71	83	295	3.77	0.85	4.42	<i>Xestia c-nigrum</i>	13	100
											<i>Ochropleura plecta</i>	12	100
											<i>Xestia xanthographa</i>	6	92
12	Clearing, mean part	74	0	45	55	73	166	3.95	0.92	4.29	<i>Calliteara pudibunda</i>	6	92
											<i>Habrosyne pyritoides</i>	6	92
											<i>Ochropleura plecta</i>	5	100

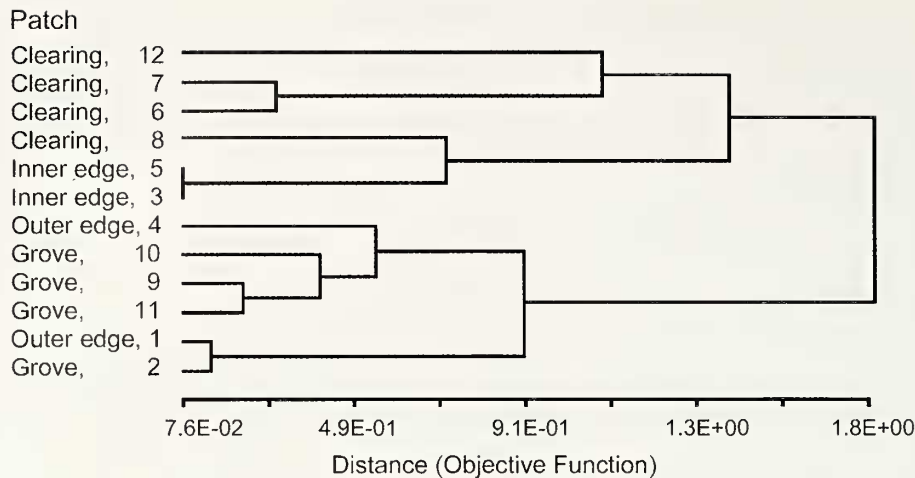


Fig. 2. Cluster analysis of similarity of Lepidoptera communities at different sites.

not vary significantly among sites of different diversity and location, whereas the absolute species number decreased with the diversity (Fig. 4; Table 2). Yet, at the sites 9, 10, and 11 outside the investigated forest, species that are specialized to conifers or deciduous trees only were more seldom, than at other sites. Consistently, species specialized to herbs as caterpillar food were more abundant at these sites.

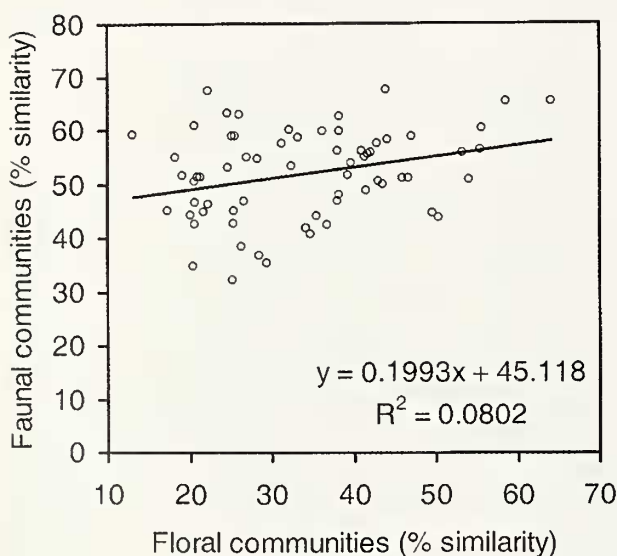


Fig. 3. Similarity of the Lepidoptera fauna at two sites, in dependency of the similarity of the flora at the same sites, respectively.

Community patterns

To find out which factors substantially regulate the occurrence of certain species at different patches, we analyzed the presence of different community patterns in the observed Lepidoptera species and in subgroups of those species. Subgroups consisted of different families, of species with different degrees of caterpillar specializations, or of species with different type of caterpillar host plants. Whereas nestedness temperature calculation identified a nested distribution in the observed 325 species of Lepidoptera, nested distributions and different forms of gradients (evenly spaced, Gleasonian, or Clementsian) were detected in the various subgroups of the Lepidoptera communities (Table 3). Checkerboards and random distributions were not observed at all. This showed that interspecific competitions, as well as purely stochastic factors were not the driving forces in community regulation. No patterns were detected in Lepidoptera species of group A, representing Hepialidae (3 species), Limacodidae (1), Zygaenidae (1), Lasiocampidae (6), Sphingidae (5), Drepanidae (10), and Geometridae (125) (Table 3). Lepidoptera species of group B, representing Notodontidae (16 species), Noctuidae (131), Pantheidae (1), Lymantriidae (4), Nolidae (5), and Arctiidae (17) showed a Clementsian distribution among patches. Different families showed different patterns, as well as did groups with different specializations of caterpillars (Table 3).

Polyphagous species were most frequent (247

Table 2. Linear regression analysis of changes in species numbers within groups with special caterpillar food resources and among patches. Patches were ordered according to decreasing total species number as obtained from nestedness calculation (as in Table 1 and in Figure 4). So, the independent variable was the species richness of the site, and the dependent variable was the proportion of Lepidoptera species which are specialized to a given group of food plants. The coefficient gives the slope of the respective regression line. Relative numbers of species within groups of food specializations are given in Figure 4.

Food specializations	Coefficient	SE	p
Regression of absolute species-numbers			
Deciduous trees	-2.6434	0.4981	0.0003
Coniferae	-0.3392	0.1136	0.0137
Herbs	-2.4895	0.6760	0.0042
Trees & bushes and/or herbs	-1.1049	0.2538	0.0014
Bushes and herbs	-1.0245	0.1500	<0.0001
Gramineae	-0.4441	0.2015	0.0521
Lichens	-0.3252	0.1377	0.0399
Others	0.0490	0.1304	0.7153
Regression of relative species-numbers			
Deciduous trees	-0.3738	0.5182	0.4872
Coniferae	-0.1419	0.0786	0.1011
Herbs	0.4216	0.6432	0.5269
Trees & bushes and/or herbs	-0.0507	0.2599	0.8493
Bushes and herbs	-0.2028	0.1270	0.1415
Gramineae	0.2816	0.1608	0.1105
Lichens	-0.0726	0.1204	0.5600
Others	0.1384	0.1106	0.2394

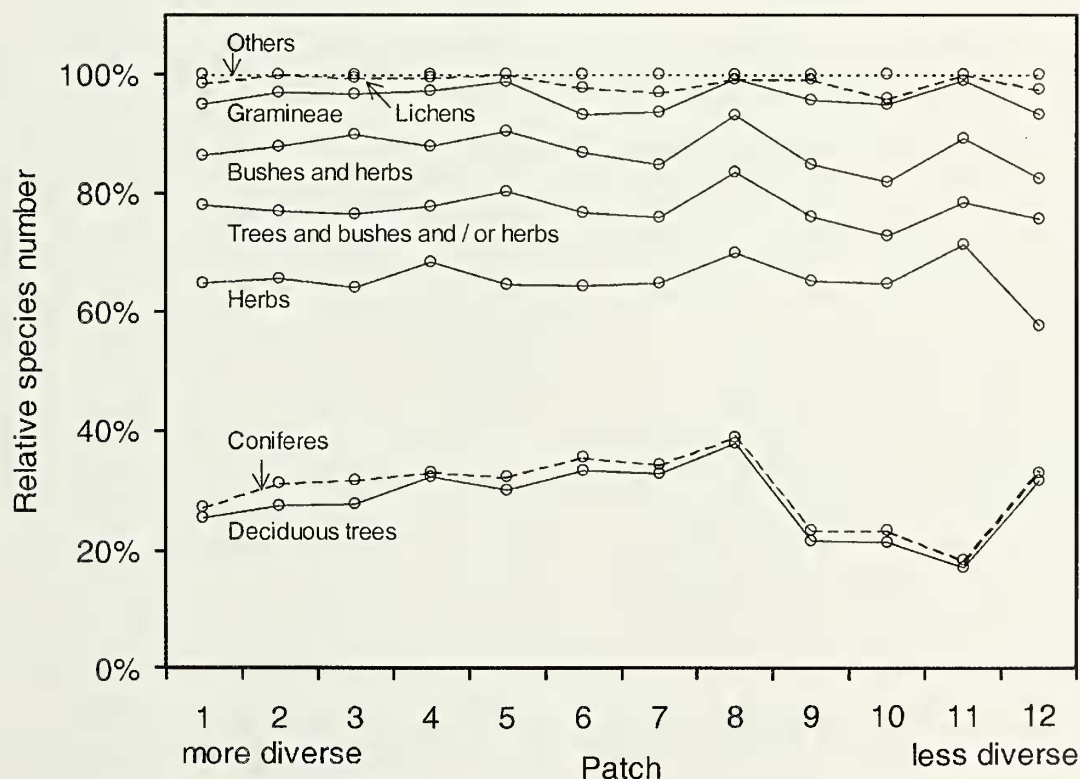


Fig. 4. Relative numbers of Lepidoptera species within groups with special caterpillar host plants (given in the figure) and at different patches. Patches are arranged from left to right according to their diversity as calculated from nestedness temperature calculator (left side, highest diversity; right side, lowest diversity).

Table 3. Community patterns of Lepidoptera species at different forest patches. Patterns were calculated according to Leibold and Mikkelsen (2002). P-levels give the significance of differences between observed and simulated patterns. (N, number of species; DF, Degree of freedom; Lepidoptera A, B, see text; *Hepialidae ++; Hepialidae, Lasiocampidae, Limacodidae, Sphingidae, Zygaenidae; **Others: Furze, Ferns, Foliage, Clematis spec.; ***Gradient: Clementisian, Gleasonian, or Evenly spaced gradients could not be distinguished in these cases)

Community	N	Embedded absences			Replacements				Community boundaries				Overall community pattern***		
		ob-served	simulated (mean + SD)	p-level	coherence	ob-served	simulated (mean + SD)	p-level	turn-over	Morita's index	Chi square	DF		p-level	Clumped or over-dispersed
Taxonomical groups															
Lepidoptera A	151	674	900.4 + 28.6	<0.0001	yes	19158	17468.7 + 8297.9	0.3189	mode-rate	0.000	128.00	149	0.8925	no	not detected
Lepidoptera B	174	963	1042.2 + 28.0	<0.0001	yes	12907	7268.0 + 3467.2	<0.0001	high	2.996	213.91	172	0.0164	clumped	Clementsian
Arctiidae	17	43	63.9 + 6.8	<0.0001	yes	357	610.7 + 177.2	<0.0001	low	1.753	29.82	14	0.0080	clumped	Nested
Drepanidae	10	16	25.3 + 4.9	<0.0001	yes	93	208.3 + 59.0	<0.0001	low	1.905	28.33	7	0.0002	clumped	Nested
Geometridae	125	488	718.4 + 21.7	<0.0001	yes	16636	13278.4 + 5026.1	0.0027	high	0.532	112.18	122	0.7268	no	Gradient
Noctuidae	131	648	760.1 + 16.2	<0.0001	yes	13565	9962.8 + 3356.4	<0.0001	high	0.000	107.00	128	0.9115	no	Gradient
Notodontidae	16	46	54.9 + 7.8	<0.0001	yes	548	391.5 + 135.8	<0.0001	high	1.333	19.67	13	0.1038	no	Gleasonian
Geometridae + Noctuidae	253	1432	1541.0 + 26.5	<0.0001	yes	32178	16082.1 + 5587.5	<0.0001	high	0.000	229.00	250	0.8256	no	Gradient
Hepialidae ++	12	41	53.4 + 6.7	<0.0001	yes	354	648.2 + 188.6	<0.0001	low	1.576	25.09	13	0.0225	clumped	Nested
Food specialisations of caterpillars															
A. Degree															
Polyphagous	247	1310	1489.1 + 32.9	<0.0001	yes	24537	14468.6 + 6742.1	<0.0001	high	1.065	246.36	245	0.4635	no	Gradient
Oligophagous	34	139	162.2 + 12.1	<0.0001	yes	3183	2014.7 + 806.4	<0.0001	high	0.943	30.86	32	0.5243	no	Gradient
Monophagous	44	198	205.8 + 11.5	0.0026	yes	2791	2608.4 + 872.6	0.3058	mode-rate	1.065	41.36	40	0.4109	no	not detected
B. Type															
Deciduous trees	93	420	516.3 + 19.5	<0.0001	yes	11561	5880.8 + 2327.6	<0.0001	high	1.970	110.36	90	0.0714	no	Gleasonian
Conifers	9	14	18.0 + 5.0	0.0006	yes	186	158.72 + 41.1	0.0029	high	1.637	17.47	6	0.0077	clumped	Clementsian
Herbs	105	448	577.1 + 25.9	<0.0001	yes	11785	6716.4 + 3091.9	<0.0001	high	1.338	109.09	102	0.2974	no	Gleasonian
Trees & bushes, herbs	41	148	200.2 + 14.7	<0.0001	yes	3285	2585.3 + 1038.5	0.0025	high	0.844	34.73	38	0.6216	no	Gradient
Bushes & herbs	32	79	146.8 + 9.3	<0.0001	yes	1374	2065.6 + 735.5	<0.0001	low	1.558	40.73	29	0.0727	no	Nested
Gramineae	27	89	117.2 + 10.7	<0.0001	yes	1047	1084.1 + 393.2	0.6419	mode-rate	0.714	18.29	24	0.7889	no	not detected
Lichens	11	14	27.0 + 5.9	<0.0001	yes	193	290.0 + 83.1	<0.0001	low	2.455	41.73	8	0.0000	clumped	Nested
Others**	9	1	6.2 + 3.0	<0.0001	yes	109	145.0 + 16.4	<0.0001	low	1.029	16.00	6	0.0138	clumped	Nested

species), compared to 34 oligophagous species and 44 monophagous ones. Polyphagous and oligophagous species showed gradients, whereas no patterns were detected in Lepidoptera species with monophagous caterpillars. Whereas nestedness indicated that patches were statistically depauperate subsets of the regional fauna, gradients showed that environmental changes between patches were responsible for different communities at that patches. Since nestedness and gradients were observed within taxonomical groups also, the related community regulating factors may act on taxonomically related species. So, species turnover should concern related species, and species loss of communities due to low patch quality may affect taxonomical subgroups of communities as well as the entity of the regional fauna.

DISCUSSION

Patch type and location

The nested distribution of 325 Lepidoptera species at 12 patches of a temperate mixed forest showed that communities at single patches represent a statistical subset of communities present at more species rich patches. Low quality patches, e.g. those of small size or unfavourable location often have small communities (Connor & McCoy 1979; Patterson & Atmar 1986; Boecklen 1997). Patch quality therefore should have been a major force regulating the community size of Lepidoptera at the studied forest patches. In the present study, forest edges showed the most species rich communities, island habitats like clearings inside the forest and groves surrounded by agricultural land had smaller communities. The diversity of butterflies on calcareous grasslands was positively correlated with habitat area, as was plant diversity, but not with habitat isolation (Steffan-Dewenter & Tscharntke 2000). Effects of spatial structure on communities depend on the mobility and dispersal strategies of the considered species. Immigration and emigration rates declined in butterfly populations with increasing patch area, while the resident fraction increased (Sutcliffe et al. 1997, Johst et al. 2002, Wahlberg et al. 2002). At fine spatial scale, Summerville et al. (2002) observed nestedness in butterflies, generated by variation in patch use by species. High flying, habitat restricted species avoided small patches, low flying and less

discriminating "ubiquitous" species were distributed more evenly. Therefore, the size of patches, as well as patch isolation, are determinants of its quality, with different significance for Lepidoptera species that differ in mobility and dispersal strategy.

Ecological adaptations

Cluster analysis revealed that the general patch type or location, inside or outside the forest, determined the present communities, with similar species composition at similar patches. Species' adaptations to environmental factors should influence the community compositions at different patches (Hutchinson 1953). Ecological adaptations and species interactions cause clumped distributions or result in gradients for communities at different patches (Clements 1916, Gleason 1926, Tilman 1982, Leibold & Mikkelsen 2002). Food specialization groups that developed by coevolution of butterflies and their larval host plants (e.g., Benson et al. 1975), represent environmental adaptations that may regulate butterfly communities (Futuyma 1976). We observed types of gradients in groups of different food specializations, indicating that the kind of food specialization influenced the distribution of the observed Lepidoptera species among patches associated to forests. Yet, with increasing similarity of plant species growing at two sites, the faunal similarity of those two sites did not increase significantly. Also, the relative number of Lepidoptera species at different sites that are specialized to different caterpillar host plants, did not vary significantly among sites of different diversity and location. Futuyma & Gould (1979) already observed that the correspondence between faunal similarity and plant affinity is not strong. The complexity of distribution of insects over plants indicated that insects responded to many factors that differentiated plant species in a deciduous forest. Ecological adaptations, and a low quality of spatial habitat characteristics possibly may lead to an overlay of nestedness and gradients in local communities. The similarity of flora and fauna at a patch may then be limited despite the ecological adaptations, e.g. of caterpillars to host plants.

Generalists and specialists

Differences in the ecological specialization may influence the relative abundance of closely related

species (Brown 1984). Generalists will be abundant where they occur, and will occupy a large geographic range, because they can tolerate a broad environmental spectrum. Specialists, which are more restricted in the resources and microhabitats they can use, should be locally rare and narrowly distributed. A few studies provide support for the ecological specialization hypothesis (e.g. Gaston 1988, Inkinen 1994, Jonsen & Fahrig 1997), whereas others do not (e.g., Hanski et al. 1993). Monophagous, oligophagous and polyphagous butterfly species showed differential responses to the area of grassland habitats with respect to species richness. The slope of species-area relationships increased with food plant specialization (Steffan-Dewenter & Tscharnke 2000). Along a gradient of human disturbance in grassland habitats, butterfly species richness was more strongly correlated with the number of specialist species than with that of generalists, and generalists were more widely distributed over communities than were the specialists (Kitahara et al. 2000). Consideration of the scale of a species' resource specialization (within or among habitats) appears to be key to understanding the relationships between resource specialization, resource availability, and a species' abundance and distribution (Hughes 2000). In our fine spatial scale investigation gradients were present among communities of polyphagous as well as of oligophagous species, but not in monophagous Lepidoptera caterpillars. The kind of food specialization, but not its degree may therefore significantly contribute to community regulation in Lepidoptera, when different kinds of habitats, forest, edges and groves are compared. The extent of differences of compared habitats should then decide, whether the kind and extent of food specialization contributes to community changes among habitats.

We conclude that in the studied forest system the patch location (isolated or at habitat edges) had most influence on the habitat quality, and resulted in nested distributions of Lepidoptera species among habitats, with species loss at low quality patches. Ecological adaptations of caterpillars to host plants produced gradients in communities among different patch types, with the scale of resource specialization being less important as a regulator. Interspecific competition, resulting in checkerboard patterns, was not observed to influence significantly the community structure. Stochastic effects, e.g., due to dispersal by wind, habitat size, and spatial barriers between island

habitats, should cause random patterns, which also were not observed in the present investigation. Similarly, in acid peatland butterflies of the Lake Superior drainage basin of Wisconsin communities deviated from random at small (<50 km) habitat extents (Nekola & Kraft 2002).

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